BIOLOGICAL CONTROL

Parasitism Characteristics of Two Phorid Fly Species in Relation to Their Host, the Leaf-Cutting Ant *Atta laevigata* (Smith) (Hymenoptera: Formicidae)

MARCOS A.L. BRAGANÇA[1], ATHAYDE TONHASCA JR.[2] AND DENISE D.O. MOREIRA[2]

[1]Centro Universitário de Porto Nacional, Fundação Universidade do Tocantins, C. postal 25, 77500-000, Porto Nacional, TO, e-mail: malbr@uol.com.br
[2]Centro de Ciências e Tecnologias Agropecuárias, Universidade Estadual do Norte Fluminense, Av. Alberto Lamego 2000, 28015-620, Campos dos Goytacazes, RJ

Neotropical Entomology 31(2):241-244 (2002)

Características de Parasitismo de Duas Espécies de Forídeos em Relação ao seu Hospedeiro, a Saúva *Atta laevigata* (Smith) (Hymenoptera: Formicidae)

RESUMO - As saúvas *Atta sexdens* (L.) e *Atta laevigata* (Smith) são consideradas sérias pragas para a agricultura e reflorestamento no Brasil. Estas saúvas são parasitadas pelos forídeos *Neodohrniphora tonhascai* Brown e *Neodohrniphora erthali* Brown (Diptera: Phoridae), respectivamente. O potencial de parasitismo de *N. tonhascai* em relação ao seu hospedeiro foi previamente investigado, mas não há informações equivalentes para *N. erthali.* Os objetivos deste estudo foram avaliar o comportamento de oviposição e algumas características biológicas de *N. erthali* em relação ao seu hospedeiro e determinar o potencial de oviposição de *N. tonhascai* para *A. laevigata*, já que em muitas áreas da região Sudeste ninhos de *A. sexdens* e *A. laevigata* são encontrados próximos uns dos outros. Os dados foram obtidos a partir de fêmeas de *N. erthali* e *N. tonhascai* coletadas no campo em Viçosa (Minas Gerais) e liberadas em uma câmara de observação colocada entre um ninho de *A. laevigata* de laboratório e sua arena de forrageamento. *N. tonhascai* levou menos tempo selecionando seus hospedeiros, atacou mais formigas e causou maiores níveis de parasitismo do que *N. erthali.* Não foi possível determinar se *A. laevigata* é parasitada por *N. tonhascai* no campo, mas o sucesso reprodutivo de *N. tonhascai* em laboratório demonstrou que *A. laevigata* é hospedeiro adequado para este parasióide. Os tipos de defesa demonstrados por *A. laevigata* contra ambas espécies de forídeos foram marcadamente diferentes, o que sugere que forrageadoras tomam medidas defensivas específicas de modo a reduzir a possibilidade de parasitismo por moscas forídeas.

PALAVRAS-CHAVE: Attini, *Neodohrniphora tonhascai, Neodohrniphora erthali,* parasitóide, controle biológico.

ABSTRACT - The leaf-cutting ants *Atta sexdens* (L.) and *Atta laevigata* (Smith) constitute serious pests of agriculture and forestry in Brazil. These ants are parasitized by the phorids *Neodohrniphora tonhascai* Brown and *Neodohrniphora erthali* Brown (Diptera: Phoridae), respectively. The parasitic potential of *N. tonhascai* against its host has been previously investigated, but no equivalent information is available for *N. erthali.* The objectives of this study were to evaluate the oviposition behavior and some biological characteristics of *N. erthali* in relation to its host and to determine the parasitic potential of *N. tonhascai* against *A. laevigata,* considering that in many parts of southeastern Brazil nests of *A. sexdens* and *A. laevigata* are found in close proximity of each other. These data were obtained from female *N. erthali* and *N. tonhascai* collected in the field in Viçosa (Minas Gerais State) and released singly in an observation chamber placed between a laboratory nest of *A. laevigata* and its foraging arena. *Neodohrniphora tonhascai* took less time selecting its hosts, attacked more ants and had greater rate of parasitism in relation to *N. erthali.* We could not establish whether *A. laevigata* is parasitized by *N. tonhascai* in the field, but the reproductive success of *N. tonhascai* in the laboratory demonstrated that *A. laevigata* is a suitable host to this parasitoid. The types of defense displayed by *A. laevigata* against both phorid species were markedly different, and these results suggest that foragers take specific defensive steps in order to reduce the possibility of parasitism by phorid flies.

KEY WORDS: Attini, *Neodohrniphora tonhascai, Neodohrniphora erthali,* parasitoid, biological control.

Throughout most of their range, *Atta* spp. leaf-cutting ants are parasitized by flies of the genus *Neodohrniphora* (Diptera: Phoridae) (Prado 1976, Disney 1994, Brown 2001). These flies pursue and attack the larger foragers walking along trails, but nearby ants are also disturbed by flies' attacking bouts. *Neodohrniphora* have been implicated in the diel shift of foraging activity exhibited by *Atta cephalotes* (L.) (Orr 1992, Feener & Brown 1993) and in the reduction of the forager force size of *Atta sexdens* (L.) (Bragança *et al.* 1998, Tonhasca & Bragança 2000). When exposed to a *Neodohrniphora* species, young *A. sexdens* colonies (less than 1-year old) stop completely their foraging activity within five minutes of initial contact with the parasitoids (D.D.O. Moreira, unpubl.). In older colonies, *A. sexdens* foragers react to the presence of these flies by abandoning their loads and returning to the nest (Bragança *et al.* 1998). Consequently, the occurrence of *Neodohrniphora* represents a disruptive factor in the foraging of *Atta* leaf-cutting ants.

Atta sexdens and *Atta laevigata* (Smith) are two of the most common leaf-cutting ants in Brazil, and both represent serious pests of agriculture and forestry (Fowler *et al.* 1989). In Viçosa, Minas Gerais State, Brazil (20°45'S, 42°51'W), these ants are parasitized by *Neodohrniphora tonhascai* Brown and *Neodohrniphora erthali* Brown, respectively. Like other *Atta*-parasitizing *Neodohrniphora* (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Orr 1992, Feener & Brown 1993), *N. tonhascai* attacks the head of the larger workers. Its behavior and parasitic characteristics in relation to *A. sexdens* have been investigated by Tonhasca (1996), where it was incorrectly named *Neodohrniphora declinata* Borgmeier, and by Bragança *et al.* (1998), where it was referred to as *Neodohrniphora* sp. No equivalent information is available for *N. erthali.*

The objectives of this study were to investigate the oviposition behavior and some biological characteristics of *N. erthali* related to its host and to determine the parasitic potential of *N. tonhascai* against *A. laevigata*. Many ant-parasitizing phorids are host specific (Disney 1994), but at least one *Neodohrniphora* species is believed to attack more than one *Atta* species (Brown 2001). Because nests of *A. sexdens* and *A. laevigata* occur in close proximity to each other in Viçosa as well as in many parts of southeastern Brazil, it could be possible for *N. tonhascai,* a species whose effects on *A. sexdens* are known, to utilize *A. laevigata* workers as host.

Material and Methods

Between 1st and 18th June 1999, 16 *N. tonhascai* females hovering over *A. sexdens* foraging trails were collected from several nests in the field. Flies were taken to the laboratory and released individually inside an observation chamber placed between a 2.5-year-old *A. laevigata* nest and a foraging arena. Bragança *et al.* (1998) described this experimental setting in detail. Fly's and ants' behavior was observed for 1h, then the fly was removed. Another phorid was released when the ants resumed their normal foraging rhythm. Ants attacked by parasitoids were removed, marked with paint on their thorax and returned to the observation chamber after 20-30 min. The same procedure was used for 15 *N. erthali* females collected from *A. laevigata* nests between 3rd and 9th July. Another 10 *N. tonhascai* were collected between 15th and 18th July, and 13 *N. erthali* between 3rd and 5th August to repeat the observations with a second *A. laevigata* nest of similar size and age of the previous one.

All *N. tonhascai* attacked the ants almost immediately after being released in the chamber, whereas only 10 *N. erthali* attacked the ants from either nest. To obtain more ants parasitized by this species, several additional releases of two to six *N. erthali* females were made along with 25 to 70 *A. laevigata* foragers in an observation chamber that was not connected to a nest. Ants were selected at random from each colony separately, but individuals with head widths smaller than about 1.7 mm (which was the minimum size of ants attacked by both parasitoids) were discarded. Ants and phorids were kept in the chamber for 15-24h. Afterwards, all ants were removed from the chamber, marked with paint on the thorax and returned to their nests after 20 to 30 min. In a 8-day period, 32 phorids and 325 ants from the two nests were released.

Dead ants parasitized by phorids in the laboratory are deposited by nestmates in the colony's refuse pile (Tonhasca *et al.* 2001). For 15 days subsequent to the parasitoid releases, dead ants with head widths larger than 1.7 mm were removed daily from the refuse pile and placed in an environmental chamber (26.5 ± 0.5°C, 85 ± 5% RH, L00:D24). Parasitism by both species was detected by the presence of a single puparium between the ant's mandibles (Tonhasca 1996). Parasitized ants were placed individually in glass tubes stopped with cotton, which were kept inside the environmental chamber until emergence of adult flies.

In the field, *N. erthali* are clearly larger than *N. tonhascai.* Ant-parasitizing phorids prefer larger individuals, a possible adaptation to increase their chances of survival and reproductive success (Feener 1987). To evaluate the effect of host size on the emergence performance of both phorid species, a factorial analysis of variance (with species and presence of puparium as factors) was performed on the data on size of dead ants recovered from the refuse pile. These variables were obtained by measuring ants' head width to the nearest 0.1 mm.

Results and Discussion

The attacking behavior of *N. tonhascai* and defensive behavior of threatened ants were similar to those described for *A. sexdens* (Tonhasca 1996, Bragança *et al.* 1998). This fly approaches the ant from its front or sides, apparently introducing the ovipositor in the posterior part of the host's head. Threatened ants may run away, try to fend off attacking bouts or protect the back of their heads with their legs. *N. erthali* on the other hand approaches the host only from its back and introduces the ovipositor in the final portion of the ant's gaster, apparently in the anal opening. Ants threatened by *N. erthali* lean on their middle and posterior legs, lift their bodies and curl their gaster inward to avoid oviposition while remaining stationary or walking slowly. They also try to "kick" the approaching fly with the posterior legs. We did not observe attacks by *N. tonhascai* against loaded

ants, but six of the 31 observed attacks by *N. erthali* were made against ants carrying leaf fragments. However, *N. tonhascai* was a more efficient parasitoid. Of the 127 attacks registered for the 26 flies released in the chamber, 46.5% resulted in puparia. There were only 31 attacks for the 28 *N. erthali*, of which 19.4% resulted in puparia.

The presence of *N. erthali* puparia between the ant mandibles indicates that the larvae migrate from the gaster to the head capsule, where resources for larval development are abundant. Adult flies emerged about 35 days after oviposition. The interaction effect between phorid species and the presence of puparium was not statistically significant, but *N. erthali* selected significantly larger ants ($F = 45.20$, $P<0.001$, d.f. = 1,269) in comparison with *N. tonhascai* (Table 1). The analysis also indicated that head widths of ants parasitized by both phorid species were larger ($F = 17.49$, $P<0.01$, d.f. = 1,269) than head sizes of ants attacked but not parasitized (Table 1). The results from both nests were combined for this analysis because the average forager size in the first nest (2.2±0.7 mm) and second nest (2.4±0.7 mm) were not significantly different according to a t-test ($t = 1.05$, $P = 0.30$, d.f. = 61).

Table 1. Means ± s.d. of head width (mm) of *A. laevigata* attacked by two *Neodohrniphora* species.

Species	Heads with puparium	Heads without puparium
N. tonhascai	3.21 ± 0.44 (n = 56)	2.99 ± 0.55 (n = 55)
N. erthali	3.82 ± 0.81 (n = 39)	3.41 ± 0.55 (n = 123)

Two important conclusions were reached from this research. First, *N. tonhascai* collected from *A. sexdens* trails not only were able to parasitize *A. laevigata,* but were also more efficient parasitoids than *N. erthali.* Despite avoiding ants carrying leaf fragments, *N. tonhascai* took less time selecting hosts, attacked more ants and had greater rate of parasitism in relation to *N. erthali.* Because *A. laevigata* was the only host available to *N. tonhascai* in these tests, we could not conclude that *A. laevigata* is parasitized by this phorid in the field. Nonetheless, the reproductive success of *N. tonhascai* demonstrated that *A. laevigata* is a suitable host for this parasitoid. Both *Neodohrniphora* species selected larger foragers for oviposition, a common trend among phorids. In fact, success of puparia formation for both species was related to host size. Because the average size of *Atta* workers in laboratory is smaller than in the field (unpubl.), *N. erthali* may have been less efficient because of reduced availability of hosts of adequate size.

The second noteworthy conclusion of this study is that the type of defense displayed by individual foragers depends on the attacking phorid species. Although the defensive behaviors of leaf-cutting ants are similar when foragers are threatened by *Neodohrniphora* spp. that parasitize their heads (Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Orr 1992, Feener & Brown 1993, Tonhasca 1996), the response of *A. laevigata* to *N. erthali* was remarkably different. Porter *et al.* (1995) suggested that ants' protective behavior is triggered by the detection of parasitoid's wing buzzing at short range. This hypothesis implies that defenses against phorids are stereotypical responses to a generic signal such as air vibrations. However, our results indicated that ants take specific defensive steps in order to reduce the possibility of parasitism.

Acknowledgments

We thank T. Della Lucia for logistical support, D. Coracini, M. Erthal Jr. and M. Ferreira for helping with field and laboratory work, and B.V. Brown for identifying the phorids. M. Bragança was supported by a grant from FAPERJ and A. Tonhasca received funds from the International Foundation for Science.

Literature Cited

Bragança, M.A.L., A. Tonhasca Jr. & T.M.C. Della Lucia. 1998. Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp. Entomol. Exp. Appl. 89: 305-311.

Brown, B.V. 2001. Taxonomic revision of *Neodohrniphora,* subgenus *Eibesfeldtphora* (Diptera: Phoridae). Ins. Syst. Evol. 32: 393-409.

Disney, R.H.L. 1994. Scuttle flies: the Phoridae. London, Chapman & Hall, 467p.

Eibl-Eibesfeldt, I. & E. Eibl-Eibesfeldt. 1967. Das parasitenabwehren der minima-arbeiterinnen der blattschneider-ameise (*Atta cephalotes*). Z. Tierpsychol. 24: 278-281.

Feener Jr., D.H. 1987. Size-selective oviposition in *Pseudacteon crawfordi* (Diptera: Phoridae), a parasite of fire ants. Ann. Entomol. Soc. Am. 80: 148-151.

Feener Jr., D.H. & B.V. Brown. 1993. Oviposition behavior of an ant-parasitizing fly, *Neodohrniphora curvinervis* (Diptera: Phoridae), and defense behavior by its leaf-cutting ant host *Atta cephalotes* (Hymenoptera: Formicidae). J. Ins. Behav. 6: 675-688.

Fowler, H.G., M.I. Pagani, O.A. da Silva, L.C. Forti, V.P. da Silva & H.L. de Vasconcelos. 1989. A pest is a pest is a pest The dilemma of Neotropical leaf-cutting ants: keystone taxa of natural ecosystems. Environ. Manag. 13: 71-675.

Orr, M.R. 1992. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. 30: 395-402.

Porter, S.D., R.K. van der Meer, M.A. Pesquero, S.

Campiolo, H.G. Fowler. 1995. *Solenopsis* (Hymenoptera: Formicidae) fire ant reactions to attacks of *Pseudacteon* flies (Diptera: Phoridae) in Southeastern Brazil. Ann. Entomol. Soc. Am. 88: 570-575.

Prado, A.P. 1976. Records and descriptions of Phorid flies, mainly of the Neotropical region (Diptera; Phoridae). Stud. Entomol. 19: 561-609.

Tonhasca Jr., A. 1996. Interactions between a parasitic fly, *Neodohrniphora declinata* (Diptera: Phoridae), and its host, the leaf-cutting ant *Atta sexdens rubropilosa* (Hymenoptera: Formicidae). Ecotropica 2: 157-164.

Tonhasca Jr., A. & M.A.L. Bragança. 2000. Effect of leaf toughness on the susceptibility of the leaf-cutting ant *Atta sexdens* to attacks of a phorid parasitoid. Insectes Soc. 47: 220-222.

Tonhasca Jr., A., M.A.L. Bragança & M. Erthal Jr. 2001. Parasitism and biology of *Myrmosicarius grandicornis* (Diptera, Phoridae) in relationship to its host, the leaf-cutting ant *Atta sexdens* (Hymenoptera, Formicidae). Insectes Soc. 48: 154-158.

Received 24/07/01. Accepted 01/05/02.